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THE EFFICIENCY OF SOME PROTECTIVE ADAPTATIONS IN SECURING INSECTS FROM BIRDS.

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DURING the past four years I have been studying the food habits of birds in the *Biological Survey* of the U. S. Department of Agriculture. Owing to the extreme kindness of my chief, Dr. C. Hart Merriam, I have now at my disposal data accumulated from the examination of the stomach contents of fifteen thousand birds. My colleague, Professor F. E. L. Beal, has given me invaluable assistance in the preparation of this paper. I am also indebted for criticism to Drs. L. O. Howard and Chas. Wardell Stiles. Messrs. Schwarz, Banks, Chittenden, and Pratt, of the Department of Agriculture, have been most kind in identifying insects.

The bulk of the insect food of birds consists of grasshoppers (Acrididæ and Locustidæ), noctuid larvæ, weevils, smaller carabids, May beetles and their allies, smaller dung beetles (Onthophagus, Hister, Atænius, and Aphodius), chrysomelids, true bugs (Heteroptera), parasitic Hymenoptera (mostly Ichneumonidæ), ants, and spiders.[1]

[1] Included thus for convenience.

Protective devices of insects do not always baffle birds, and to illustrate this I have arranged my results in the following manner:

A. Restricted Protective Coloration (Resemblance to Substratum).

I. ORTHOPTERA.

1. Grasshoppers (Locustidæ and Acrididæ), 300 species of birds.
2. Katydids (Locustidæ), brown thrasher, chippy, screech owl, great horned owl, Mississippi kite, red-shouldered hawk.
3. Walking Sticks (Diapheromera), crow blackbird, two species of cuckoos.

II. LEPIDOPTERA.

1. Measuring Worms (Geometridæ), catbird, house wren, two species of cuckoos, scarlet tanager, red-winged blackbird, cowbird, bobolink, Baltimore oriole, purple finch, indigo bird, Wilson's thrush, cedar bird, white-winged crossbill, chippy, kingbird, and other flycatchers, vireos, Carolina titmouse, and many warblers.
2. Ground-colored Cutworms (Noctuidæ), practically all insectivorous birds which feed upon the ground to any extent.
3. Longitudinally striped Caterpillars:
   (*a*) Army worm, red-headed woodpecker, flicker, and other woodpeckers, cowbird, most blackbirds, orioles, meadow lark, bobolink, English sparrow, many native sparrows, kingbird, phœbe, quail, robin, bluebird.
4. Green Caterpillars:
   (*a*) Sphinxes, catbird, blue jay, two cuckoos, white-eyed vireo, red-shouldered hawk, broad-winged hawk.
   (*b*) Ailanthus Worm, yellow-throated vireo.
   (*c*) Cabbage Worm (Pieris), chippy, robin.
   (*d*) *Telea polyphemus*, broad-winged hawk.
5. Small protectively colored moths, several species of sparrows.

III. COLEOPTERA.

1. Protectively colored Longicorns (Cerambycidæ), many woodpeckers.
   (*a*) Monohammus, great-crested flycatcher.
2. Weevils, all insectivorous birds.
3. Chlamys (Chrysomelidæ), robin, bluebird, native sparrows.

IV. HEMIPTERA.

1. Jassidæ, marsh wren, house wren, cowbird, blackbirds, great-crested flycatcher, kingbird.
2. Membracidæ, great-crested flycatcher, Brewer's blackbird.

3. Scale Insects (Coccidæ), cedar bird, woodpeckers, white-breasted nuthatch, chickadee, California bush tit.
4. *Nezara hilaris*, or Brochymena, Podisus, or Euschistus, catbird, brown thrasher, house wren, cardinal, cuckoos, blackbirds, kingbird, phœbe, great-crested flycatcher, vireos, hermit thrush, blue jay, robin, Acadian flycatcher, least flycatcher, crow, cowbird, white-bellied swallow.
5. Flat Bugs (Aradidæ), downy woodpecker.
6. *Piesma cinerea*, chickadee, white-breasted nuthatch.
7. Thread-legged Bugs (Emesidæ), golden-cheeked warbler.

V. DIPTERA (Crane Flies [Tipulidæ]), many insectivorous birds.

VI. TRICHOPTERA (Larval Caddice Flies), red-winged blackbird.

VII. ARACHNIDA.

1. Spiders (Araneida), general resemblance to substratum, practically all land birds.
2. Harvest Spiders (Phalangidæ), many birds, especially catbird, wrens, and cuckoos.

B. Special Devices — Hairs.

I. LEPIDOPTERA (LARVÆ).

1. Arctiids, robin, bluebird, catbird, sparrow hawk, cuckoos, and shrikes.
2. Gypsy Moth, blue jay, robin, chickadee, chippy, vireos, cuckoos, Baltimore oriole.
3. *Vanessa antiopa*, Baltimore oriole, cuckoos.

C. Special Devices — Stings or Poisonous Bites.

I. HYMENOPTERA.

1. Bombus, or Xylocopa, bluebird, blue jay, olive-sided flycatcher, great-crested flycatcher.
2. Honey-bee (*Apis mellifica*), wood pewee, phœbe, olive-sided flycatcher, kingbird.
3. Andrena, or Halictus, red-eyed vireo, least flycatcher, great-crested flycatcher, wood pewee, olive-sided flycatcher, kingbird, blue jay, swift, cliff swallow, white-bellied swallow, humming bird, chestnut-sided warbler, Maryland yellowthroat, blue jay.
4. Scoliids (especially Tiphia, Myzine, and Elis), English sparrow, least flycatcher, kingbird, wood pewee, cliff swallow, rough-winged swallow, barn swallow.
5. Vespa, or Polistes, red-bellied woodpecker, kingbird, yellow-bellied flycatcher.
6. Mutillidæ, Says's phœbe, western wood pewee.

II. ARACHNIDA.

1. Large Biting Spiders, many birds.
2. Scorpion, screech owl, great-horned owl, burrowing owl.

III. MYRIOPODA.

1. Lithobius and others, many birds.

D. Special Devices — Ill-Flavored, or Scented, or with Irritating Qualities.

I. HYMENOPTERA.

1. Ants, most land birds.

II. HEMIPTERA.

1. Heteroptera, all insectivorous birds.
   (*a*) Anasa, broad-winged hawk, red-shouldered hawk.
   (*b*) *Prionidus cristatus*, crow.
   (*c*) Pentatomidæ, majority of insectivorous birds.
   (*d*) Hygrotrechus, song sparrow.

III. COLEOPTERA.

1. Carabidæ:
   (*a*) Smaller Carabidæ, such as Amara, Anisodactylus, Agonoderus, Pterostichus, Cratacanthus, Bembidium, and smaller Harpalus, all insectivorous birds.
   (*b*) *Harpalus caliginosus*, or *pennsylvanicus*, crow, blackbirds, meadow lark, catbird, brown thrasher, robin, kingbird, Cassin's kingbird, dickcissel.
   (*c*) Carabus, bluebird and crow, crow blackbird.
   (*d*) Cychrus, crow blackbird.
   (*e*) *Galerita janus*, bluebird, blue jay, young crow blackbirds.
   (*f*) Chlænius, crow, crow blackbird, catbird, bluebird.
   (*g*) *Calosoma scrutator*, or *calidum*, crow, crow blackbird, red-headed woodpecker, blue jay, cuckoo.
2. Histeridæ and Scarabæidæ Laparosticti (Aphodius, Atænius Onthophagus, Canthon) (foul from food), most insectivorous birds.
3. Silphidæ (Silpha or Necrophorus), crow, loggerhead shrike, kingbird.
4. Some Tenebrionidæ:
   (*a*) Nyctobates, catbird.
5. Coccinellidæ, flycatcher, red-eyed vireo, song sparrow, marsh wren, Lewis's woodpecker.
6. Chrysomelidæ:
   (*a*) Potato Beetle (*Doryphora 10-lineata*), wood thrush, rose-breasted grosbeak, quail, crow, cuckoo, catbird.

(*b*) *Diabrotica 12-punctata*, Attwater's grouse, blue jay, catbird, red-eyed vireo, cliff swallow, brown thrasher, purple martin, phœbe, yellow-bellied flycatcher.

(*c*) *Galerucella luteola*, phœbe, cedar bird.

7. Lampyridæ (Chauliognathus), see warning coloration.

IV. NEUROPTERA.

1. Chrysopa, great-crested flycatcher, song sparrow.

V. ARACHNIDA.

1. Harvest Spiders (Phalangidæ), many birds.

VI. MYRIOPODA.

1. Millipedes, many birds.

E. Warning Coloration.

I. LEPIDOPTERA.

1. Orgyia, larval, two species of cuckoos.
2. *Datana ministra* larval, two species of cuckoos.
3. *Anisota senatoria* larval, two species of cuckoos and robin.
4. Isabella caterpillar, loggerhead shrike, robin, sparrow hawk.
5. Showy butterflies, catbird, kingbird, wood pewee, purple martin, scarlet tanager, crow blackbird, cuckoo, English sparrow, song sparrow.

II. HYMENOPTERA.

1. Agapostemon and other metallic green small bees, flycatchers, humming bird, and a dozen other species.
2. Chrysis, many birds.
3. *Vespa maculata*, yellow-bellied flycatcher.
4. *Vespa germanica*, kingbird.
5. Elis and Myzine, see under stinging insects.
6. *Tremex columba*, blue jay, olive-sided flycatcher, loggerhead shrike, red-eyed vireo, night hawk.

III. COLEOPTERA.

1. Carabidæ:
   (*a*) Calosoma, Chlænius, Pterostichus, see under irritating fluids.
   (*b*) *Lebia grandis*, kingbird.
2. Lampyridæ:
   (*a*) Chauliognathus, kingbird, wood pewee, phœbe, cliff swallow, catbird.
3. Scarabæidæ:
   (*a*) *Allorhina nitida*, blackbirds, crow, catbird, blue jay, red-headed woodpecker.

(*b*) *Euphoria fulgida*, blackbirds, crow, blue jay, kingbird.
(*c*) Godsmith Beetle (*Cotalpa lanigera*), blue jay, yellow-billed cuckoo, purple martin.
(*d*) *Pelidnota punctata*, blue jay.
(*e*) *Phanæus carnifex*, blackbirds, crow, catbird, brown thrasher, great-crested flycatcher.
(*f*) *Bolbocerus farctus*, kingbird, catbird.

4. Chrysomelidæ:
   (*a*) *Systena tæniata*, song sparrow, chippy, yellow-winged sparrow, field sparrow, Maryland yellowthroat.
   (*b*) *Odontota dorsalis*, catbird, great-crested flycatcher, robin, orchard oriole, Baltimore oriole, Carolina wren, song sparrow, chippy, chewink, cardinal, cedar bird, yellow warbler, wood pewee.
   (*c*) Small metallic green beetles (especially Chætocnema, Crepidodera, Dibolia, Donacia, Graphops), a great many birds.
   (*d*) Doryphora, Diabrotica, see ill-flavored insects.
   (*e*) *Chrysomela pulchra*, kingbird.
   (*f*) *Lema trilineata*, phœbe, least flycatcher, Acadian flycatcher.
   (*g*) *Lina scripta*, cuckoo.
   (*h*) *Crioceris asparagi*, kingbird.
   (*i*) *Gastroidea polygoni*, crow blackbird, catbird.
   (*j*) *Coptocycla signifera*, crow blackbird.
5. Cerambycidae:
   (*a*) Anthophylax, kingbird.
   (*b*) *Neoclytus caprea*, catbird.
6. Malachiidæ (*Collops quadrimaculatus*), phœbe.
7. Nitidulidæ (*Ips fasciatus*), white-bellied swallow.
8. Buprestidæ (metallic colored), red-bellied woodpecker, great-crested fly-catcher, black-billed cuckoo, cardinal.
9. Cucujidæ (*Cucujus cavipes*), great-crested flycatcher.
10. Coccinelidæ, see under ill-flavored insects.
11. Silphidæ (Necrophorus), see under ill-flavored insects.
12. Byrrhidæ, robin, bluebird, native sparrows.
13. Tiger Beetles (Cicindelidæ), metallic colored, quite a number of birds.

IV. DIPTERA (METALLIC COLORED), catbird, swallows, flycatchers, etc.

V. ODONATA (BLUE AGRION), green heron.

VI. ARANEIDA (ARGIOPE), dickcissel.

F. Protective Mimicry.

I. HYMENOPTERA (RESEMBLANCE AT LEAST).
   1. ICHNEUMONIDÆ, most birds.
   2. Siricidæ, see under warning coloration.
   3. Chrysidæ, mimic Stinging Bees, many birds.

II. DIPTERA.
   1. Syrphus Fly, mimics a Yellow Jacket, most flycatchers.
   2. Drone Fly, mimics a Honey-bee, kingbird, phœbe.

III. TRICHOPTERA.
   1. Caddice Flies, said to mimic Millers, many birds.

IV. COLEOPTERA.
   1. Casnonia (Carabid), mimics an Ant, house wren, song sparrow.
   2. Some Cerambycidæ, mimic Wasps:
      (*a*) Typocerus, blue jay, wood pewee.
      (*b*) *Leptura zebra*, red-eyed vireo, kingbird.
      (*c*) Cyllene, wood pewee.
      (*d*) *Neoclytus erythrocephalus*, song sparrow.
      (*e*) *Strangalia luteicornis*, kingbird.
   3. Staphylinidæ, mimic Wasps, many birds.

The above tabulated matter is merely a collection of records, fragmentary and incomplete. It does not show the frequency with which any species of insect is selected for food by any particular bird, and consequently is liable to erroneous interpretation.

Insects which resemble the Substratum upon which they rest.

We will first proceed to ascertain whether those insects which exhibit protective coloration in its restrictive sense, that is, those that resemble what they rest upon, always baffle birds. We wish to determine how efficient this protective adaptation is; in a word, we desire to measure its working force.

In *Natural Selection*, p. 63, Wallace says: "The whole order of Orthoptera, *i.e.*, grasshoppers, locusts, crickets, etc., are protected by their colors, harmonizing with that of the vegetation or the soil on which they live." . . . On the next page he goes on to state: "We do not adduce any more examples to show how important are the details of form and

of coloring in animals, and that their very existence may often depend upon their being by these means concealed from their enemies." I am surprised to find that grasshoppers (Acrididæ and Locustidæ) in spite of their protective coloration are eaten by over three hundred species of birds in the United States.

Grasshoppers are eaten in large quantities by birds. They amount during the year, exclusive of the winter months, to 19 per cent of the volume of the insect food in the catbird, 25 per cent in the house wren, and 40 per cent in the meadow lark. In August 67 per cent of the red-winged blackbird's food consists of grasshoppers, and for the same month this staple amounts to 70 per cent in the meadow lark. For the two months of May and June grasshoppers amount to 80 per cent of the insect food of the loggerhead shrike. Of course, in the tropics, where we have such marvelous special adaptations as are found in the Mantidæ and leaf insects, there must be the most wonderful efficiency.

It may be argued that many of the grasshoppers eaten belong to the less protected forms, but we know that *Dissosteira carolina*, which is practically invisible on the ground, is selected, and that it is no uncommon thing to find the remains of several Locustidæ in stomachs. Whether these insects were taken when they were at rest, that is, when protective coloration is effective, is the great point and, so far as I have experimented with several birds, there seems every reason to believe that Acrididæ at least do not, when at rest, successfully baffle birds. I put several admirably protected grasshoppers (Acrididæ) among the fallen brown oak leaves, where I found them with the greatest difficulty, in a cage with a song sparrow, a junco, and white-throated sparrows. The legs of the insects had been pulled off, so they kept perfectly still, but the birds instantly saw and seized the grasshoppers. I tried the same experiment in a large cage with mocking birds and got the same results.

The great bulk of grasshoppers eaten by birds are Acrididæ, but stomachs containing a dozen Locustidæ are not at all uncommon. The Locustidæ most commonly selected belong to the genera Scudderia, Orchelimum, and Xiphidium. Of

the more especially protected Locustidæ we have the leaf-resembling katydids eaten by a number of birds of prey, and there are three cases on record of crow blackbirds eating full-grown walking-sticks (Diapheromera).

If we consider the number of grasshoppers (Melanopus) eaten by individual birds, it is interesting to note that the jaws and other remains of 48 grasshoppers were found in the digestive organs of one wood duck, 59 in a robin, and in a Swainson's hawk 133. These figures come from Professor Aughey, who made a study of the effect of birds upon an invasion of *Melanopus spretus*. Of course these insects were at the time so much in excess of all other species that it is only natural that they should have been taken for food. The same line of argument is applicable in the eastern United States during August and September, when many birds are subsisting to a large extent upon the abundant supply of orthopterous food. However this may be, it is a fact that in June and July, when there is no such superabundance of Orthoptera, birds nevertheless select principally from this order of insects to secure food to rear their young upon. I have no data to offer which will show how often any given grasshopper is passed over by a bird, and thus protected by its coloration being in conformity with its surroundings. I know full well that if these insects were colored a flaming red they would be much more conspicuous to us, and probably to the birds. From the little field work that I have been able to do, it seems to me probable that most grasshoppers are captured by birds not on the wing, but at rest or when moving very sluggishly. This summer, while collecting in a hayfield, I found it difficult to secure specimens of *Melanopus femur-rubrum*, which was very abundant. The insects arose at every step or so, but the instant they settled they became almost invisible. Protective coloration commenced to act as soon as they alighted. I watched an orchard oriole hunting in this field, but I failed to see any insects fly before her, though she at the time was feeding three young almost exclusively upon grasshoppers. From the little that I could see of a yellow-winged sparrow which was also feeding young, I was unable to see her flush

grasshoppers. This negative evidence is of little use. I had hoped to be able to make extended observations and perform a large series of experiments with caged birds, but have been unable to do so, and now can only offer a fragmentary contribution to this most interesting subject. Orthoptera along the Atlantic seaboard, in spite of their protective coloration, are fed upon extensively by practically all of our birds, and the degree of efficiency of their protective adaptation is probably low as compared with that enjoyed by many other insects.

The stomachs sent in to the Department of Agriculture are not accompanied with data as to the available supply of insect food. This material shows a much greater consumption of grasshoppers than I was able to find in stomachs which I collected in fields where grasshoppers were not up to their usual abundance. Although nestling birds were being reared largely upon grasshoppers, the parent birds were feeding upon insects which were less common than the grasshoppers.

Of the larvæ of Lepidoptera, the twig-resembling Geometridæ, which show a marvelous degree of special protective resemblance, are eaten by more than a score of birds of the eastern United States. The ground-colored cutworms, that so closely simulate the earth in which they live, are eaten by practically all the land birds which feed to any extent upon the ground. In the middle of May, 1898, I found that birds were feeding extensively upon Agrotis. The larvæ were abundant in the earth or under stones, but I saw none crawling about. Because of their nocturnal habits and protective coloration it is difficult to understand how the birds secured so many of them. During June and July, 1898, on a certain farm, I was unable to collect many specimens of noctuids and other protectively colored smooth caterpillars, but the birds seemed to have no trouble in finding them. Later in the season, however, during an infestation of *Protoparce carolina* in a tobacco field, no birds were found to select these protectively colored larvæ. Adult Lepidoptera as compared with the larvæ can hardly be considered as forming any significant part of bird food. The smaller inconspicuous moths seem to be relished by caged birds. These insects are occasionally preyed upon by the

majority of land birds. I have collected scores of birds in places where noctuid, crambid, pyralid, and geometrid moths were abundant, and not found a trace of a moth in any of the birds' stomachs. These insects, whether protected by their harmonizing coloration or by some other adaptation, are more immune from the attacks of birds than grasshoppers.

Weevils have a combination of protective devices; they are very hard-shelled, and they resemble either little stones or clods of earth. Moreover, they drop to the ground and feign death. Authors have dilated at length upon these admirable protective devices of weevils. But it seems to me that here we find the working force of protective adaptations at about as low an ebb as anywhere, for not only are these insects not immune, but they are eaten in great numbers by all insectivorous birds whose food we know anything about. It is not uncommon to find in the stomachs of such granivorous birds as sparrows as many as a dozen weevils.

32 Balaninus from downy woodpecker.
40 Sitones from crow blackbird.
109 *Dorytomus mucidus* from a hairy woodpecker.

The question with these weevils, as with grasshoppers, is whether they are caught while they are still and protective coloration is acting. I think that any one who has observed English sparrows and blackbirds hunting weevils on lawns can certify that many weevils are picked up from the vegetation or ground. Of course with flycatchers the case is often different, and the insects are taken on the wing. Experiments with caged birds should be carried on on a large scale. I confess that I have only experimented with one kind of bird and one kind of weevil. I sunk *Sitones hispidulus* in sand of its own color, so that only the back of the insect was uncovered. I could not see it, but the insect was seen as readily by my song sparrow as if it had been flaming red, white, and blue. In the dozen times this experiment was repeated the bird flew instantly and seized and swallowed the weevil.

I shot 45 birds on May 13 and 18, 1898, on a farm where I was only able to collect a single weevil. One-third of these birds had fed upon Sitones, Phytonomus, and Tanymecus.

One can hardly say in the face of these facts that the protective adaptations of these weevils is highly efficient in securing them from the attacks of birds. It seems as though birds became accustomed to discriminating between weevils and gravel stones, and, knowing how palatable weevils are, in spite of their hard covering, the birds seek them out, and even pass over apparently less protected insects.

In passing to the Hemiptera one finds that the homopterous division affords very little food supply to birds. The Jassids, as far as my experiments go, seem to be relished, but nevertheless they are not in large quantities habitually eaten by birds, in spite of the fact that they are very abundant. Whether it is their protective resemblance or some other device which secures them this degree of immunity from attack, I cannot say. The Aphididæ are still more protected. They are distasteful to catbirds, and, I imagine, to many other species.

Scale insects have been found only in the stomachs of several birds collected in winter, and in Baltimore orioles taken in summer. The true bugs (Heteroptera), which are protectively colored, are eaten by a great many birds.

Ground-colored spiders, whether taken while at rest or when running, are fed to the young of practically all the land birds of the eastern United States.

Hairs.

I next come to the consideration of special devices, such as, for instance, a hairy covering of the integument as we have in many caterpillars. With the exception of our two species of cuckoos no species of bird in the eastern United States, so far as I am aware, makes a business of feeding upon hairy caterpillars. The loggerhead shrike occasionally preys upon these insects, but with practically all other birds it is only in exceptional cases that a hairy caterpillar is eaten. I remember seeing an old pear tree which was infested with *Hyphantria cunea*. These insects were not at all molested, in spite of the fact that the old tree was tenanted by three broods of birds at the time — kingbirds, orchard orioles, and English sparrows.

An orchard oriole's nest with three young in another tree had a nest of hairy caterpillars within four inches of it. The hairiness of caterpillars seems to secure them from the attacks of birds more effectually than do any of the particular protective coloration devices thus far considered.

Stings.

The stings of Hymenoptera also serve as an effective protective device. A young sparrow, in whose mouth I inserted a small bee (Andrena), was stung in the throat, soon became very much affected, and finally I killed it to relieve its sufferings. A caged chewink seized a honey-bee, pecked it well and then swallowed it, but died within fifteen minutes. Mr. Benton, of the Agricultural Department, tells me that he had to give up raising ducks, because those just hatched ate honey-bees about the apiaries and were fatally stung. Nevertheless, I had a caged blue jay that would eat such large bees as Bombus and *Xylocopa virginica.* Flycatchers habitually feed upon stinging Hymenoptera, particularly upon Scoliids. The same is true of swallows, and the English sparrow is very fond of Tiphia and Myzine. Other birds occasionally take stinging Hymenoptera, less often large Apinæ. On May 18, 1898, I shot a catbird near a willow tree in which many bees were humming about the flowers, and the bird contained three small bees. The bird had a large supply of food, cutworms, beetles, etc., to choose from, but, nevertheless, took bees. It has been pointed out by Beddard that stinging Hymenoptera, in addition to being warningly colored, have disagreeable odors and tastes; it is also to be noted that many stinging Hymenoptera are not warningly colored, as the theory of protective coloration would, of necessity, demand them to be.

Among the ants there is a large division, the Myrmicidæ (the stinging ants). The smaller species of this division are eaten by a great many birds. Some of these ants have thorns on their abdomens which are said by Wallace to protect them from birds. More than any other protection perhaps is the formic acid which ants contain, but the efficiency of this device

seems low in cases where, as in the flicker, we find stomachs containing 3000 ants. The stingless ants pretend to sting, but there are many birds that they do not deceive.

There are two records of the caterpillar of the Io moth having been eaten by the yellow-billed cuckoo. In one instance no less than seven of these large stinging larvæ were taken from a single stomach.

It is plain that from my facts I interpret, not cases of protection and non-protection, but cases of greater and lesser efficiency of protective devices.

Ill-Flavored or with Irritating Qualities.

In the Heteroptera, particularly in the Pentatomidæ, we have insects emitting vile stenches. In speaking of the Pentatomidæ Comstock says: "It should not be concluded, however, that only members of this family possess this disagreeable odor; for most of the Heteroptera protect themselves by rendering their bodies unpalatable in this way. Doubtless birds soon learn this fact and leave such bugs alone." An English sparrow raised from the nest refused a Brochymena, and a song sparrow did not eat one of these insects, but ate with relish Lygus and small stinking Reduviids. In the examination of song-sparrows' stomachs I often find remains of Pentatomids, and I know of no insectivorous bird that does not eat Heteroptera. Catbirds and thrashers (caged) relish Brochymena. Blackbirds and crows frequently contain from four to ten Euschistus. The stench may protect bugs from some birds, but it certainly does not secure complete immunity from but very few birds of eastern United States. The lace-wing fly is about as nauseating an insect as I know of; yet it was greedily devoured by a caged song sparrow, and has been taken from the stomach of a great-crested flycatcher. Phalangidæ have a sickening stench, but they are eaten by many birds, particularly by house wrens and cuckoos. Millipedes come in the same category and are relished by birds.

In coming to the protective adaptations of Coleoptera we find a greater efficiency of the actual working of protective devices,

especially in the families Coccinellidæ and Chrysomelidæ. In the Coccinellidæ we have showy insects, ill-scented or flavored, that are eaten by but very few birds — the flycatchers and swallows; and hence here is a whole family which conforms well with the theory of warning coloration. Blue jays, song sparrows, thrashers, and other birds, when caged, refuse even when hungry these little beetles.

Turning to the family Chrysomelidæ, we have the potato beetle, that is refused by the catbird, blue jay, and song sparrow, and disgorged after being eaten by the thrasher. Several other examples might be mentioned, but when we come to the green Chrysomelids, especially the smaller ones, the efficiency is greatly reduced; the metallic tints that were supposed to always warn off birds are constantly disregarded, and we have many birds eating green Chrysomelids. Diabroticas are not often eaten and have been refused by song sparrows, but were greedily devoured by catbirds and thrashers. The elm leaf-beetle is almost protectively colored, but relies upon something else, perhaps its secretions, for protection. This insect is refused by many birds, but is occasionally eaten by the cedar bird. *Galerucella sagittaria* is also avoided.

The smaller Carabid beetles, whether stinking or not, seem to be eaten by practically all land birds. A song sparrow which was fed with a Chlænius was ill for twenty minutes, and then next day picked at but refused another. This same bird relished the stinking Nebria and Agonoderus. Crows, blackbirds, and jays relish *Calosoma scrutator.*

Crows and blackbirds have been known to feed Galerita, a very strong-smelling beetle, to their young. It seems incredible that birds should be able to eat Galerita, Calosoma, Carabus, and the larger Cychrus. Many birds eat species of Harpalus; the crow and the blackbirds are especially fond of *Harpalus caliginosus* and *pennsylvanicus.*

There are a score of smaller Carabidæ and Chrysomelidæ (metallicly and conspicuously colored) which are habitually eaten by birds that have an abundance of other insect food to pick from. On one farm I found fourteen species of birds preying upon *Odontata dorsalis*, and seven upon *Systena tæniata.*

With the Lampyrid beetles the stenches, whether or not coupled with conspicuous coloration, are more effective. Telephorus is occasionally eaten, but Photinus, if eaten at all, is taken only very rarely. Chauliognathus, though often so very abundant, is not eaten by many birds, but several species of flycatchers and swallows select this insect. Experiments with caged birds, catbirds, and blue jays showed that this insect was regarded unfavorably.

Warning Coloration and Mimicry.

The writers on protective coloration, especially Wallace, have stated that birds avoid insects that have metallic colors. Thus metallic coloration becomes synonymous with warning coloration. Although this is doubtless true in some cases, there are others in which it seems otherwise. The metallic beetles (Buprestidæ), certain Cicindelidæ, *Allorhina nitida*, *Euphoria fulgida*, *Cotalpa lanigera*, and Phanæus are relished by many of our common birds. And, further, it may be added that the metallic-colored flies, *Lucilia cæsar* and others, are found in large quantities in the stomachs of flycatchers and swallows; that is, in the stomachs of all birds that are swift enough to capture them. Large showy bugs colored like *Murgantia histrionica* are usually avoided by birds. A captive song sparrow refused a Murgantia, but a white-throated sparrow devoured it greedily. It is very seldom that I run across the remains of orange and black or red and black bugs during stomach examinations.

So much has been written on the subject of protective coloration of adult Lepidoptera that I cannot, even in this preliminary paper, pass over such an important chapter without stating some of the problems that here concern the student of protective coloration. I realize that in this order we have, especially in the tropics, very efficient methods of protection from birds, as has been shown by the investigations of Bates, Belt, Wallace, Triman, Poulton, and Beddard; but in the eastern United States the cases of efficient mimicry do not show up quite so well, for the reason that there are not yet any records

of birds habitually preying upon butterflies. In fact the same question has been agitated in the discussion following the reading of Mr. Dixey's most interesting paper at the London Entomological Society; and it was found that comparatively few members had ever seen birds take butterflies. In the eastern United States there have been hardly more than a dozen published records of birds seen in the act of taking butterflies. In fact birds, so far as I have observed, seem to make no practice of giving chase to the butterflies that float about them as they busily catch other insects. In fact butterflies seem to be avoided, whether they are indifferently colored, protectively colored or mimetic, or warningly colored. It is said by Wallace that our milkweed butterfly is imitated by Limenitis, which thus escapes capture; but, as none of our butterflies are persecuted, it seems strange if mimicry has actually been aimed at. Beddard has shown that there are difficulties in the theory of protective mimicry, from the fact that mimicking and mimicked forms are eaten, and that, in certain cases, instances of apparently useless mimicry occur. Beddard also shows some inconsistencies in the current interpretation of the theory of warning coloration. He shows that certain warningly colored papilio larvæ have a habit of not relying on their warning coloration, but conceal themselves. He further concludes, in speaking of warning coloration: "There are so many other easier ways of defense, and one would imagine that the action of natural selection would proceed along the line of least resistance." Some criticism in a measure adverse to protective mimicry is brought out in a paper entitled "Mimetisme," by M. C. Piepers, in the *Proceedings of the International Zoölogical Congress*, 1895, pp. 460–476. The greatest piece of work in actually putting the protective coloration theory to test has been accomplished by Frank Finn. The results of this investigation are published in the *Journal of the Asiatic Society of Bengal*, Vol. LXVI, Part II, No. 4, 1897. The author performed hundreds of experiments in feeding birds with butterflies. Mimetic, warningly colored, and non-protected butterflies were used. The birds employed included *Liothrix luteus*, *Otocompsa emerisa*,

Molpastes leucotis, M. bengalensis, Pycnontus sinensis, Cratceropus canorus, Acridotheres tristis, Anthracoceros, Mesia argentauris, Dissemurus paradiseus, Dicrurus ater, Sturna menzbieri, Kittacincla macrura, Chloropsis aurifrons, Malacias capistrata, Turnix taigoor. The experiments were made in cages and in an aviary. Mr. Finn's conclusions are:

"1. That there is a general appetite for butterflies among insectivorous birds, even though they are rarely seen, when wild, to attack them.

"2. That many, probably most species, dislike, if not intensely, at any rate in comparison with other butterflies, the warningly colored Danainæ, *Acrea violæ*, *Delias eucharis*, and *Papilio aristolochiæ*, of these the last being the most distasteful and the Danianæ the least so.

"3. That the mimics of these are at any rate relatively palatable, and that the mimicry is commonly effectual under natural conditions.

"4. That each bird has to separately acquire its experience, and well remembers what it has learned."

That, therefore, on the whole, the theory of Wallace and Bates is supported in this and my former papers, so far as they deal with birds (and with the one mammal used). Professor Poulton's suggestion that animals may be forced by hunger to eat unpalatable forms is also more than confirmed, as the unpalatable forms were commonly eaten without the stimulus of actual hunger — generally also, I may add, without signs of dislike."

Mr. Finn's elaborate series of experiments have proved that non-protectively colored butterflies are preferred to warningly colored ones. He notes the avoidance of the protected forms, but, in cases where they are eaten, fails to detect any signs of actual distaste. In fact there is, it seems to me, no hard and fast line between distaste and lack of preference. There is, however, in the mind of every one a distinct difference. For instance, I prefer beef to mutton, but this does not signify that mutton is distasteful to me. On the other hand, quinine and kerosene are actually distasteful. In applying the same standard to the case of the warningly colored butterflies I

should not, in spite of their not being preferred by birds, have called them distasteful. In my own experiments I have found that certain beetles are avoided to such an extent that birds will not touch them even when they are very hungry. Laying aside this quibble of the degree of distastefulness, it is clear that the lack of preference, however slight, is all that is required by the theory of protective coloration.

It would be exceedingly interesting to know to what extent the species of birds which Mr. Finn experimented with, feed upon butterflies when at liberty. I know of no native species of birds in the United States which habitually prey upon butterflies.

In the Linnean Society's journal, *Zoölogy*, Vol. XXVI, there is an article entitled "Natural Selection the Cause of Mimetic Resemblance and Common Warning Colours," by Professor Edward B. Poulton. The scope and aims of this masterly paper are so entirely different from those of my little contribution that I will not discuss it here. I have experimented in feeding butterflies to birds just enough to become confused. My song sparrow ate a *Papilio turnus;* a blue jay found a *Colias philodice* distasteful; while catbirds relished *Vanessa antiopa.* In spite of these experiments I must conclude, from the examination of stomach contents and field work, that butterflies are comparatively immune from the attacks of birds of the eastern United States.

Caddice flies are supposed to mimic small moths for protection, but they, nevertheless, are eaten by many birds, even when plenty of other insects are obtainable.

In the Diptera and Hymenoptera we have such swift-flying insects that birds have great difficulty in catching them. The Muscidæ are relished by most birds, but only the flycatchers and swallows are swift enough to catch them. The kingbird eats the Eristalis fly that mimics the honey-bee and also other mimicking Syrphus flies.

The parasitic Hymenoptera (Ichneumonids) are said to mimic the stinging ones, but they are eaten by many birds. It has also been supposed that many of our flower-infesting Cerambycid beetles mimic Scoliid wasps. However this may be, the

beetles are seldom eaten. A wasp-like Cerambycid *Neoclytus erythrocephalus*, however, was relished by a song sparrow. It is maintained also that Staphylinid beetles mimic stinging Hymenoptera; nevertheless, they are relished by a good many birds.

One of the most salient difficulties in the actual working of the theory of protective mimicry is met with when the insects eaten by the kingbird are examined. Here one finds that the yellow and black Hymenoptera, imitating Syrphidæ, are eaten by the kingbird. Further, that *Eristalis tenax*, which mimics the honey-bee so perfectly, is also taken. These facts, though bad enough for the effectiveness of the mimicry, are not to be mentioned in the same category with still another. The kingbird is well known to feed upon honey-bees, but, strangest of all, the bird seeks only the drones. This would lead one to infer that if a bird was keen enough to tell the different castes of bees apart on the wing, it would not be likely, to any considerable extent, to be humbugged by mimetic resemblance.

Mr. Benton, of the Department of Agriculture, tells me that domesticated fowls can tell the difference between drones and working honey-bees. Hens will stand by a hive and seize the drones as they come out, but do not touch the workers. In fact hens make a certain alarm cluck when they suddenly run across a worker.

Miscellaneous Matter.

Size often determines whether a given insect shall be eaten by a particular bird. The *Papilo turnus* which my caged song sparrow killed after several minutes of hard work would undoubtedly have escaped had it been outside, and a sphinx moth which my catbirds killed after a quarter of an hour's struggle would certainly have gotten away. So with many beetles. Small species can be easily managed; but a catbird, for instance, with a *Passalus cornutus* is helpless, while a blue jay has the strength to break the insect to pieces and then eat it. I gave a *Hydrophilus triangularis* to my blue jay. His beak glanced off the insect's back again and again, but finally he

struck it on the ventral side so as to disable the beetle, and then he hammered it to pieces and ate the soft parts.

The quick flight of Odonata and many Diptera prevent them from being captured in any quantities. I can offer no reason why the rose chafer is not a favorite article of bird food. I have often found this insect abundant where I have collected birds, but, with the exception of the kingbird, no bird seems fond of it. Catbirds captive and at liberty avoid the Colorado potato beetle. One adult catbird, however, shot where there was an abundance of food, had eaten a potato beetle. On the other hand, catbirds in captivity relish *Diabroctica 12-punctata* but avoid it when at liberty. I could give a number of other examples equally perplexing.

Conclusions.

It appears to me that certain writers upon protective adaptations have identified their specific cases as coming under the ban of the theory of protective adaptations in so far as they coincide with or do not run counter to a statement of Darwin's, in which he says that a necessary deduction from the theory of the definite facts of organic nature is that no special organ, no characteristic form or marking, no peculiarities of instinct or of habit, no relations between species or between groups of species can exist, but which must now be or once have been useful to the individuals which possess them. This statement of Darwin's has comparatively so little intention and is capable of such great extension that it forms a secure bulwark over which no armies opposed in the least degree to the theory of protective adaptations can ever hope to pass. It is as good as saying that every conceivable phase of animal life is a protective adaptation (a statement which I cannot deny). But it seems to me that there are different degrees of protective adaptations — that some are much more effective than others. There is need of some standard of the efficiency of protective adaptations, *i.e.*, a measure of their working forces. Some of the writers on the subject have led one to suppose that a good many protective devices secure almost complete immunity

from the attacks of birds; while other investigators have been tempted, when they found in particular instances that facts, apparently, did not coincide with current views, to abandon the theory entirely. Butler fully realizes the fact that very broad generalizations are almost impossible, since, as he states, there is no insect that will not be refused at some time by some birds, and there are no insects that one can be sure will not be eaten by some birds under certain conditions. Beddard, after reviewing his own experiments and those of Wallace, Butler, Weir, Morgan, Weisemann, and Poulton, states that there is the greatest difficulty in drawing broad conclusions; and he, moreover, points out the fact that, in the case of the insects that are refused, it is not usually on account of color alone, but more often for the reason of a collection of disagreeable attributes, such as spininess, conspicuous coloration, and bad flavor.

It seems to me that many caterpillars that have warning coloration are refused in part because they are hairy, because birds refuse inconspicuous hairy caterpillars as well as showy ones; and, moreover, cuckoos which feed upon hairy caterpillars do not avoid those of conspicuous pattern. Nevertheless, the hairiness of caterpillars must be ranked as highly efficient in protecting them from birds. The showy, ill-flavored Coccinellidæ may be awarded almost as high a place, and the elm-leaf beetle, not showily colored, should be rated even higher. The Diabroticas, Doryphoras, and several other similar beetles should be also reckoned as possessing comparative immunity from many birds.

Wherein lies the reason for the comparatively high scale of immunity of plant lice and rose chafers (Macrodactylus) I know not. It is a fact that the smaller Carabidæ, such as Anisodactylus, Amara, Nebria, Agonoderus, and Harpalus, are eaten much more frequently than Galerita, Carabus, and Calosoma. And from birds the size of sparrows and smaller it is doubtless true that large Carabids are well protected. Nevertheless, we know that the large insectivorous birds are not baffled by the irritating fluids these insects emit.

Among the Lampyridæ, Chauliognathus appears to have

almost as high a degree of immunity as Coccinellidæ. The quick-flying Diptera seem to be not far behind in the scale of immunity from the attacks of birds, but with aculeate Hymenoptera there is somewhat of a drop, and when we get to the parasitic Hymenoptera we find that they are eaten by many birds and apparently relished.

Among the Coleoptera, Cyllene and other conspicuous flower-loving Cerambycids are seldom found by the examiner of birds' stomachs. Meloids of the type Epicauta have, in their secretions, an efficient protection against birds, but they are exceptions. Thus, in each of five kingbirds' stomachs, taken in one locality, there were thirteen of these beetles. Butterflies, in the scale of efficiency of their protection, will rank a good deal higher than even Coccinellidæ. Homoptera, with the exception of Cicadas and Jassids, are seldom eaten. Dragon-flies are not often caught when they have once been safely launched on the wing, but May flies and Caddice flies are terribly persecuted.

Apparently irrespective of coloration, the smaller Carabidæ, and particularly all abundant Scarabæidæ, except the rose chafer, are eagerly sought after for food by most insectivorous birds.

From the study of the insectivorous food of birds, it seems to me that biologists have not yet entirely elucidated all the details of the nature of the adaptations of insects which are most potently protective. Some investigators seem to reason from the standpoint of man: that since an insect tastes bad in our mouth, therefore it must be distasteful to a bird. What is one man's meat may be another man's poison. Consequently it seems to me that the human criteria are not necessarily adapted to suit the avian case. It does not follow that, since a stink bug nauseates our stomach and irritates our tongue, it will produce a like effect on a crow. Hence there appears to be need of a little more avian psychology before it is possible to entirely coincide with certain current views upon protective adaptations.

Numerous species of bugs and beetles which, in addition to being protectively colored, possess ill-smelling, bad-tasting, and

irritating secretions, would naturally be supposed by some writers to be avoided generally by nearly all birds, *but they are habitually eaten* by many birds of the eastern United States. This would lead one to infer that protective adaptations in our country are not always so efficient in securing insects from birds as has been commonly held.

The fact that beetles and other insects which are gaudily colored — and consequently are supposed to be protected from birds — are greedily devoured by many birds, appears to show that warning coloration is not always as efficient as alleged, and one is almost led to believe that, because of this inefficiency of warning coloration in many cases, protective mimicry has been in some instances overestimated. Even the theory of protective coloration in its restrictive sense, when pitted against some facts, apparently loses a little of its luster in certain cases; and we are forced to admit that factors may exist which sometimes nullify its action, so that the alleged protective coloration is not the all-important factor in securing an insect from extermination, as some earlier naturalists have supposed, but that there are other equally important factors that demand consideration. That is to say, coloration is not all, but only one of the determining elements.